The European ankylosaur record: a review

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Keywords: Ankylosauria, late Middle Jurassic to Late Cretaceous, Struthiosaurinae, Europe

Abstract
Ankylosaur skeletal remains and tracks from the European Middle Jurassic to Upper Cretaceous are reviewed here. Whereas the Jurassic material assigned to four species are known mostly by isolated elements, the Early Cretaceous record is more complete, including better cranial material and some partial skeletons. Jurassic to Early Cretaceous material is known almost exclusively from western Europe. The first half of the Late Cretaceous begins with a 12 My long gap without any ankylosaur material from the continent (not counting the earliest Cenomanian, dubious '*Acanthopholis*' material). The first systematically valuable Late Cretaceous assemblages are from the Santonian of Hungary. The Campano-Maastrichtian record is only represented by different species of *Struthiosaurus* both in the western and eastern parts of the European archipelago. Characters used to define the recently resurrected European clade Struthiosaurinae by Kirkland and colleagues are also reviewed.

Introduction
Although the earliest evidence of ankylosaurs in Europe goes back into the late Middle Jurassic (GALTON 1980a, 1983a) and their record extends up to the Maastrichtian (e.g. NOPCSA 1929, PEREDA-SUBERBIOLA 1993a, 1999, PEREDA-SUBERBIOLA et al. 1995, CODREA et al. 2002, GARCIA & PEREDA-SUBERBIOLA 2003, ŐSI et al. 2014a), remains of these quadruped, low-level browsers are sporadical and relatively poorly known from the continent. Most of the remains are associated, or in a few cases, articulated elements of the postcranium generally with the lack of associated cranial elements. Skull or mandibular bones, being the most important elements to clarify taxonomic assignment and systematic relationships, are in many cases either isolated specimens or non-overlapping, fragmentary remains making comparison highly questionable. Whereas the western European record is characterized by a wide temporal range (ca. 90 My, though not always continuously, Fig. 1), ankylosaur remains east from the River Rhein are known almost exclusively from Santonian to Maastrichtian deposits (ca. 20 My, but see JURCSÁK & KESSLER 1991). In addition, at least in the later part of record diversity is further biased by the endemic nature of continental vertebrate faunas, especially in eastern Europe, a phenomenon supported by dwarf, relict and sometimes quite unusual forms (BENTON et al. 2010, STEIN et al. 2010, ŐSI et al. 2012, 2014b, CSIKI-SAVA et al. 2015).
The aim of the present study is to give a brief overview of the European ankylosaur record, and, in the light of new discoveries and recent phylogenetic works, to present the affinities and some further anatomical comments on some taxa. Characters used to resurrect the European clade Struthiosaurinae (KIRKLAND et al. 2013) are also reviewed. Catalogue numbers of the different specimens are not listed in this paper, but can be found in the related papers cited either in the summary of an individual species or in Table 1.

The Jurassic record

Ankylosaur remains from Jurassic sediments of Europe are extremely rare and most of them are isolated bones (for a detailed overview see GALTON 1983a). Four different species have been identified, but a big problem is the almost complete lack of overlapping elements between these species, since only some osteoderms can be compared between *Dracopelta zbyszewskii* and *Sarcolestes leedsi*. Whereas CARPENTER (2001) regarded all of them as *nomina dubia*, VICKARYOUS et al. (2004) listed *Sarcolestes* and *Dracopelta* as Ankylosauria *incertae sedis* and *Cryptodraco* and *Priodontognathus* as *nomina dubia*.

Sarcolestes leedsi

The oldest representative of European ankylosaurs based on skeletal remains is *Sarcolestes leedsi* known by a fragmentary but well preserved left mandible from the Middle Callovian Lower Oxford Clay, England (LYDEKKER 1893, GALTON 1980a, 1983a, b, Fig. 2A). According to THOMPSON et al. (2012) *S. leedsi* is certainly ankylosaurian in having a glenoid posteromedial to the mandibular adductor fossa (ch. 67), a closed mandibular fenestra (ch. 68), a sinuous ventral margin of dentary in lateral view (ch. 71), and an osteoderm on the lateral side of the postdentary part of the mandible (ch. 91). Mandibular remains among the few Jurasssic ankylosaurs are known in *Gargoyleosaurus parkpinorum* from the Kimmeridgian of Wyoming, USA (KILBOURNE & CARPENTER 2005) and *Tianchiasaurus* (DONG 1993) from the Middle Jurassic of China. *Sarcolestes* differs from *Gargoyleosaurus* in having a ventrally more bent anterior part of the dentary and a medially more convex tooth row bordered labially by a wide shelf. On the other hand, the latter form has a relatively higher coronoid process indicating a relatively greater mass of external adductor muscles in this species.

Besides the holotype mandible, three osteoderms from the Middle Jurassic of England have been referred to *Sarcolestes* (GALTON 1983b, 1994). One of them, certainly a median element, was first interpreted as covering the frontoparietal region of the skull (GALTON 1983b:fig. 1I-N), that was later reinterpreted as a median osteoderm sitted somewhere along the vertebral column (GALTON 1994). The second osteoderm, being similar to the previous element, is also a median scute. Both of these scutes have at least one side with complex, concave margins (GALTON 1994:fig. 1B, D). Among ankylosaurs, median osteoderms (as a single unit without the median suture between two obviously fused elemens as seen in some ankylosaurids or *Edmontonia*) are quite rare (for armour compositions see YOUNG 1935, COOMBS & MARYANSKA 1990, BLOWS 2001, FORD 2000, FORD & KIRKLAND 2001). Regarding nodosaurids, the Santonian *Hungarosaurus* from Hungary possesses a large and massive, boomerang-shaped osteoderm with concave posterior margin and two conical spikes (Fig. 3J) laterally on its dorsal surface (ŐSI 2005). This element should have been in a median position, perhaps in the sacral or anterior caudal region of the body (ŐSI & MAKÁDI 2009), since it was found together with the pelvic elements of the fourth skeleton of this species. A common feature of these median elements is that their lateral side ends in a narrow, slightly pointed, supposedly posterolaterally oriented part bordering the concave, posterior margin.

Cryptodraco eumerus and *Dracopelta zbyszewskii*

Cryptodraco eumerus (SEELEY 1869, LYDEKKER 1889) from the Middle Upper Oxfordian of England is known on the basis of a single right femur (GALTON 1980a, 1983a). Following THOMPSON et al. (2012) this femur is most similar to that of nodosaurid ankylosaurs in having a femoral head well separated from greater trochanter by a distinct notch (ch. 150).

Dracopelta zbyszewskii from the Kimmeridgian of Portugal has been described on the basis of a partial rib cage with armour (GALTON 1980b, Fig. 2D). GALTON (1980b) pointed out that the wide variety in the form of individual osteoderms along the lateral side of the rib cage and the connecting or sometimes overlapping position of the osteoderms occur only in

ankylosaurs. In addition to this material, an articulated partial autopodium, probably a right manus with three digits have been assigned to the holotype and referred to *D. zbyszewskii*. The specimen is one of the few articulated autopodia of an ankylosaur, and indicates an autopodium morphology quite similar to those of later, more derived species (PEREDA-SUBERBIOLA et al. 2005).
Besides these Late Jurassic ankylosaurian remains, some osteoderms from the Kimmeridgian (DELAIR 1973) and a caudal vertebra from the Tithonian of England (CASEY 1963) have been referred to Ankylosauria indet (GALTON 1983a).

Priodontognathus phillipsii
Priodontognathus phillipsii is known based on a left maxilla from the Upper Jurassic or Lower Cretaceous of England (SEELEY 1875, GALTON 1980c, 1983a, Fig. 2B, C). Its systematic position is highly controversial. SEELEY (1869) described it originally as *Iguanodon phillipsii*, and later, under the name *P. phillipsii*, he referred it to stegosaurs (SEELEY 1893). OSTROM (1970) concluded that it might be stegosaurian or ankylosaurian and GALTON (1980c) referred it to ankylosaurs. More recent workers (e.g. CARPENTER 2001a, VICKARYOUS et al. 2004) regarded it as nomen dubium. The features against its ankylosaurian affinity are as follows: 1) it lacks a rugose ornamentation on the lateral surface (ch. 77 of THOMPSON et al. 2012, Fig. 2B), [Attila! Eddig már több ch. xx sorszám szerepelt, de nem tudni, hogy honnét valók ezek a soszámok. Kirklandéi? Vagy ezek mind Thompson munkájára vonatkoznak, amelyre itt először történik említés?] although GALTON (1980c) noted that most of the lateral surface had been eroded; 2) the buccal shelf is weakly developed only slightly overhanging the maxillary tooth row. In all ankylosaurs, including the Kimmeridgian *Gargoyleosaurus*, this shelf is well developed laterally, widely overhanging the relatively thin base of the maxillary tooth row. Whereas GALTON (1980c) noted that the replacement teeth of *Priodontognathus* are similar to ankylosaurs in various aspects, BARRETT (2001) concluded that they are rather unusual among ankylosaurs showing some similarities with those of *Sceliodsaurus harrisonii*. Unfortunately, it is not clear, if the antorbital fenestra, clearly lacking in all ankylosaurs, is present on the specimen or the whole posterodorsal segment of the maxilla is for the articulation of the jugal and lacrimal. At present, it is ambiguous if *Priodontognathus* is an ankylosaurian or a basal thyreophoran, but the latter option is at least supported by the inset of the maxillary tooth row as synapomorphy of the group (ch. 25 of THOMPSON et al. 2012), even if it is not so pronounced.

Ankylosaur tracks
Accepting the Berriasian age of the ankylosaur track from the Purbeck beds in England (ENSOM 1987, LOCKLEY 1991, LOCKLEY & MEYER 2000, MCCREA et al. 2001), one possible occurrence of Jurassic ankylosaur (or stegosaur) tracks has to be mentioned from Aalenian-Bajocian of Yorkshire, England (MCCREA et al. 2001). Named as *Deltapodus brodericki*, they have been originally described as sauropod tracks (WHYTE & ROMANO 1994), but later on LOCKLEY et al. (1994) referred them to as possible ankylosaurian. If this latter interpretation is correct than these prints record the earliest indication of ankylosaurs in Europe.

Early Cretaceous record
Compared to the Jurassic and Late Cretaceous assemblages, the Early Cretaceous record of ankylosaurs is more abundant and diverse including at least five valid species of four genera (according to VICKARYOUS et al. 2004). On the other hand, cranial elements definitely belonging to these species are poorly known. Whereas CARPENTER (2001) referred *Hylaeosaurus* and the two species of *Polacanthus* (*P. foxii* and *P. rudgwickensis*) to Polacanthidae, later authors (VICKARYOUS et al. 2004) did not find support for this clade in

their phylogenetic analysis, and THOMPSON et al. (2012) referred these species, together with *Anoplosaurus curtonotus*, among nodosaurids. VICKARYOUS et al. (2004) regarded *Hylaeosaurus* and the two species of *Polacanthus* as Ankylosauria *incertae sedis*, and *Anoplosaurus curtonotus* as provisional Ankylosauria *incertae sedis*. The fifth Early Cretaceous species *Europelta carbonensis*, together with *A. curtonotus* and the Late Cretaceous forms (see below) has been assigned to Struthiosaurinae, a monophyletic clade of European nodosaurids (KIRKLAND et al. 2013). Besides the skeletal remians of ankylosaurs, trackways assigned to this group has to be also mentioned.

Hylaeosaurus armatus

The stratigraphically oldest species is *Hylaeosaurus armatus* from the Valanginian of England known by two partial skeletons including a great part of the postcranium and some poorly known skull elements (MANTELL 1833, 1841, OWEN 1858, PEREDA-SUBERBIOLA 1993b, CARPENTER 2001b), in addition to some referred isolated elements from western Europe (e.g. BARRETT 1996 and see PEREDA-SUBERBIOLA 1993b for an overview). Based on its holotype (Fig. 2E) and a referred specimen (BMNH 3789, MANTELL 1849) this species is the only European form with a partly articulated armour preserved in the presacral and caudal regions (articulated sacral armour is only known in *Polacanthus foxii*, see Fig. 2F).

Isolated bones tentatively referred to *Hylaeosaurus* outside from England have been described from other western European localities as well. A distal humerus and a fragmentary elongated bone, being possibly a cervical spike, has been documented from the Valanginian of western Germany (SACHS & HORNUNG 2013). Some metapodia and a possible spike-like osteoderm from the Berriasian of Cornet, Romania (JURCSÁK & KESSLER 1991, POSMOSANU 2003) have been referred to *Hylaeosaurus*, but the remains are too fragmentary for a more precize taxonomic assignment and regarded here as cf. Ankylosauria indet. Nevertheless, if this material is truly ankylosaurian, then the are the only ankylosaurian bone elements prior to the Santonian in Central and East Europe.

Polacanthus foxii

Polacanthus foxii was a medium- to large-sized ankylosaur known from Barremian to Aptian deposits of England (mostly from the Wealden of the Isle of Wight, but other localities on the mainland as well) and Spain (OWEN 1865, HULKE 1882, 1888, BLOWS 1982, 1987, PEREDA-SUBERBIOLA 1994, NAISH & MARTILL 2001). The holotype specimen consists of a partial postcranium with dorsal vertebre and ribs, synsacrum with pelvic region, numerous caudal vertebrae, hindlimb elements, ossified tendons, and dermal armour including the ossified sacral shield and various osteoderms with different morphology. Among the referred specimens a partial skeleton including some cranial elements, different parts of the vertebral column with a partial synsacrum, pelvic girdle remains and numerous elements of the dermal armour is the most complete one (BLOWS 1987). Besides these articulated/associated specimens, a fragmentary ilium with armour (type of *Polacanthus becklesi* HENNIG, 1924) and numerous isolated elements have been referred to this species (e.g. LEE 1843, DELAIR 1982, NOPCSA 1929, GASULLA et al. 2003, see PEREDA-SUBERBIOLA 1994 for an overview). Among the latter ones, a fragmentary basicranium from the Barremian of the Isle of Wight, described by NORMAN & FAIERS (1996), has to be mentioned (but see CARPENTER & KIRKLAND 1998). The only overlapping element between this specimen and the cranial remains described by BLOWS (1987) would be the supraoccipital. NORMAN & FAIERS (1996), however, could not identify this bone in the BLOWS collection and questioned the affinity of that specimen. Isolated teeth referred to *Polacanthus* are also known from Barremian deposits of the Isle of Wight (NAISH & MARTILL 2001: text-fig. 7.7). Since the type specimens does

not have teeth, the identity of these isolated teeth are only based on their similar stratigraphic occurrences.
Ankylosaurian remains referred to *Polacanthus* outside from England are known from different localities of Spain. SANZ (1983) reported a hollow-based, spike-like osteoderm from the Barremian to Aptian of Burgos, Spain. Two caudal spike-like osteoderms (PEREDA-SUBERBIOLA et al. 1999) and a more diverse material including dorsal vertebrae and ribs, a fragmentary sacrum and different types of osteoderms have been assigned to this genus (PEREDA-SUBERBIOLA et al. 2007). Specimens reported from France cannot be assigned to *Polacanthus* (PEREDA-SUBERBIOLA 1993b). The only cranial material referred to *Polacanthus* outside of England is two teeth described by CANUDO et al. (2004). The more complete specimen, however, clearly differs from the one illustrated by NAISH & MARTILL (2001) in the absence of a cingulum and the distal curvature of the crown, that might be related to taxonomic difference.
Based on detailed comparisons, BLOWS (1987) and PEREDA-SUBERBIOLA (1991, 1994) suggested synonymy of the Barremian aged North American *Hoplitosaurus* with *Polacanthus* providing the first evidence of a European ankylosaur outside of the continent. However, later authors (CARPENTER & KIRKLAND 1998, CARPENTER 2001, VICKARYOUS et al. 2004, THOMPSON et al. 2012) rejected this hypothesis, although noting close affinities of the two taxa.

Polacanthus rudgwickensis
This recently erected species of *Polacanthus* is based on a fragmentary skeleton comprising two anterior dorsal vertebrae, several caudal fragments, a proximal end of the left scapula with a fragment of fused coracoid, distal end of a humerus, a nearly complete right tibia, rib fragments, and two osteoderms (BLOWS 1996). This species is only known from the Barremian of Sussex (unknown on the Isle of Wight, where *P. foxii* occurs) and is 30% larger than *P. foxii*. Additional, minor differences between the two species are in the morphology of the dorsal and caudal vertebrae, tibia, and presacral dermal spines (BLOWS 1996). Whereas the validity of this species has been accepted by most of the recent systematic workers (see e.g. CARPENTER 2001, VICKARYOUS et al. 2004, THOMPSON et al. 2012), its phylogenetic relationships remain controversial. CARPENTER (2001) listed it among polacanthids, VICKARYOUS et al. (2004) referred it with uncertain placement to Ankylosauria, and a more conventional analysis of THOMPSON et al. (2012) recovered it among nodosaurids, but not as the sister species *P. foxii*.

Europelta carbonensis
This recently described species is one of the most completely known ankylosaurs of Europe comprising two published (KIRKLAND et al. 2013) and three, additional, unpublished skeletons (LUIS ALCALÁ, pers. comm, 2014). The type specimen is composed of a partial skull (Fig. 2I, L) and mandible, teeth, and most of the postcranium including a quite diverse collection of osteoderms. The paratype has no cranial but mandibular material, teeth and many elements from the postcranium. The forelimb is a poorly known region in both specimens preserving only the partial humeri (KIRKLAND et al. 2013: fig. 21). The early Albian *Europelta carbonensis* is of great importance, since it fills an almost unknown horizon in the late Early Cretaceous ankylosaur record. The only considerable ankylosaur material close to this period is *Anoplosaurus curtonotus* from the British late Albian (see below), and the possibly reworked and non-diagnostic '*Acanthopolis* material' from the lowermost Cenomanian of Folkestone, England (PEREDA-SUBERBIOLA & BARRETT 1999).

Anoplosaurus curtonotus

This late Albian species from the ?Upper Gault Clay or ?Cambridge Greensand (RAWSON et al. 1978) of Cambridge, England is based on a partial skeleton including the anterior half of the left dentary with 13 alveoli (Fig. 2G, H), numerous centra from all regions of the vertebral column, dorsal ribs, a partial right scapula and both fragmentary coracoids, and various limb elements (SEELEY 1879, but see also NOPCSA 1923a, PEREDA-SUBERBIOLA & BARRETT 1999). A thyreophoran synapomorphy (SERENO 1986) recognized in the *Anoplosaurus curtonotus* material is the tooth row being sinuous in dorsal and lateral views. The shallow symphyseal ramus (less than half the maximum depth of the mandibular ramus in lateral view, THOMPSON et al. 2012, ch. 69) indicates an eurypod (stegosaurs and ankylosaurs) affinity. Although the phylogenetic analysis of THOMPSON et al. (2012) recovered *A. curtonotus* among nodosaurid ankylosaurs, none of their listed ankylosaurian or nodosaurid synapomorphic characters can be identified on the material. Nevertheless, the ventrally bending anterior end of the dentary with the first preserved alveolus very close to the symphysis, the ridge-like acromial process of scapula terminating in a knob-like eminence, and the shape and robustness of the humerus are all features suggesting its ankylosaurian affinity.

Ankylosaur tracks

Early Cretaceous footprints inferred to have been produced by ankylosaurs are known from several localities in Europe. ENSOM (1987) described ankylosaurian tracks from the Berriasian Purbeck beds of Yorkshire, England. The ankylosaurian affinity of these footprints have been supported by later authors (LOCKLEY 1991, LOCKLEY & MEYER 2000, MCCREA et al. 2001). One trackway from the Berriasian Wealden Beds of Germany, named as *Metatetrapous valdensis*, has been referred to ankylosaurs (NOPCSA 1923b, HAUBOLD 1971, MCCREA et al. 2001, HORNUNG & REICH 2014). Various ankylosaur tracks have been reported from Lower Cretaceous carbonate deposits of Italy. Hauterivian-early Barremian footprints are known from the Gargano Promontory in southern Italy (PETTI et al. 2008, SACCHI et al. 2009), and most recently a nice trackway, interpreted as ankylosaurian, has been documented from the lower Aptian shallow-marine carbonate deposits of Puglia, southern Italy (PETTI et al. 2010). Although ankylosaur skeletal remains are unknown from the central and southern parts of Europe, these footprints strongly indicate their presence in the Early Cretaceous western Tethyan archipelago.

The Late Cretaceous record

The Late Cretaceous ankylosaur record starts with a huge gap until the Santonian. The only ankylosaur material from the first half of the Late Cretaceous has been assigned to different species of *Acanthopholis* (for a review see PEREDA-SUBERBIOLA & BARRETT 1999). The type material of *Acanthopholis horridus* (Huxley 1867) was collected from the Albian-Cenomanian Cambridge Greensand of England (most probably lowermost Cenomanian, RAWSON et al. 1978) and composed of a fragmentary basicranium, three isolated teeth, a dorsal vertebra, and some osteoderms revised by PEREDA-SUBERBIOLA & BARRETT (1999). (HUXLEY listed some other elements as well, but the latter authors could not identify them). Later on, additional remains have been found and described (SEELEY 1869, 1879, LYDEKKER 1888), but their localities and their relationships to the type material and to each other are dubious. PEREDA-SUBERBIOLA & BARRETT (1999) concluded that all the five erected species of *Acanthopolis* are nomina dubia, since the material is fragmentary, non-diagnostic, and in some cases a composite of different species/individuals.

The Santonian to Maastrichtian ankylosaurian record is more complete including four different species referred to two genera. Material is not restricted to western Europe but relatively abundant in Central and East Europe as well.

Hungarosaurus tormai

Hungarosaurus tormai is the best known Late Cretaceous ankylosaur described on basis of numerous partial skeletons from the Santonian of western Hungary (ŐSI 2005). For today, altogether nine partial skeletons (Fig. 3K) and hundreds of isolated cranial and postcranial elements can be referred to this medium-sized (estimated body length 4-4.5 m) ankylosaur species. Phylogenetic analysis recovered it as a basal nodosaurid closely related to the other European form *Struthiosaurus* (ŐSI & MAKÁDI 2009, THOMPSON et al. 2012). *Hungarosaurus* was quite unique among ankylosaurs in having gracile and elongate limb elements, a forelimb-hindlimb proportion of 1:1, a hypertrophied cerebellum, and paravertebral elements. These features let us to conclude that this Santonian form have had a sophisticated cerebral coordination of posture and movement and a more cursorial locomotary habit than predicted for other ankylosaurs (ŐSI et al. 2014b). Furthermore, analysis of the wear pattern of the *in situ* mandibular teeth revealed a sophisticated tooth–tooth contact and a palinal jaw movement demonstrating a complex feeding mechanism of this nodosaurid (ŐSI et al. 2014c).

Struthiosaurus austriacus

Struthiosaurus is the most wide-spread taxon of European ankylosaurs ranging from westernmost locality of Laño, Spain to the east of Haţeg Basin, Romania. Remains of this small- to medium-sized genus are known from Santonian to Maastrichtian deposits having one of the longest temporal distribution (ca. 17 My) of an ankylosaur genus (ŐSI & PRONDVAI 2013).

The earliest discoveries of *Struthiosaurus* were the remains of *S. austriacus* from the Lower Campanian of Muthmannsdorf, eastern Austria (BUNZEL 1870, 1871, SEELEY 1881, NOPCSA 1929, PEREDA-SUBERBIOLA & GALTON 1992, 1994, 2001). Based on multiple scapulae, the Austrian material belongs to at least three different individuals representing at least two size categories (NOPCSA 1929, for a historical and taxonomic overview of this material see PEREDA-SUBERBIOLA & GALTON 2001). Cranial elements are a small (probably subadult, PEREDA-SUBERBIOLA & GALTON 1994) basicranium with partial skull roof (Fig. 3A) (plus an endocranial cast), the anterior half of a right dentary (Fig. 3B), a symphyseal end of a larger dentary, and a few teeth. The postcranial record is more abundant comprising cervical and dorsal vertebrae and ribs, pectoral (Fig. 3C) and pelvic elements, numerous elements of the fore- and hindlimbs, and various osteoderms including ossified cervical half rings (Fig. 3D) and conical spikes (Fig. 3E) with uncertain position. VICKARYOUS et al. (2004) tentatively assigned *S. austriacus* to the Nodosauridae based on the presence of a knob-like acromion. According to THOMPSON et al. (2012) the following unambiguous ankylosaurian synapomorphies can be found in this species: supratemporal fenestrae (most probably) closed (ch. 3), cranial sutures in adult specimens obliterated (ch. 17), cranial ornamentation from the elaboration of skull bones is present (ch. 77). The nodosaurid affinity is supported by the distinct notch between the femoral head and the greater trochanter (ch. 150) and by the domed parietal surface (ch. 31).

Struthiosaurus transylvanicus

Struthiosaurus transylvanicus is based on a fragmentary cranium (skull roof, occipital region, posterior and ventral parts of the orbital region, quadrates, plus an endocranial cast, Fig. 3G-I) and some additional postcranial bones (cervical dorsal and caudal vertebrae, ribs, fragmentary right scapulocoracoid, Fig. 3F) from the Maastrichtian of Haţeg Basin, Transylvania, Romania (NOPCSA 1915, 1929). Concerning the phylogenetic affinities of *S. transylvanicus* the same ankylosaurian and nodosaurid synapomorphies (except for ch. 150, see above) listed by THOMPSON et al. (2012) can be observed. On the other hand, two unambiguous

synapomorphies of Ankylosauria (presence of postorbital/squamosal and quadratojugal horns [ch. 84, 86, respecitvely]) are not present on the skull of *S. transylvanicus* suggesting the quite basal position of this species among nodosaurids.
While some authors (PEREDA-SUBERBIOLA & GALTON 1994, PARISH 2005, THOMPSON et al. 2012) regarded *S. transylvanicus* potentially synonymous with *S. austriacus*, CARPENTER (2001) and VICKARYOUS et al. (2004) distinguished the two different species. The latter opinion might be supported by the highly anysochrone stratigraphic position of the two species. *S. austriacus* is ca, 13-15 My older (early Campanian) than *S. transylvanicus* and the two species existed on two different landmasses in the western Tethyan archipelago (see CSIKA-SAVA et al. 2015). Nevertheless, the most comprehensive study on the basis of osteological traits made by PEREDA-SUBERBIOLA & GALTON (1994) could not distinguish the two species from each other.
Recently, some additional remains referred to *Struthiosaurus* has been published from the Upper Cretaceous of Transylvania including a tooth in a small jaw fragment (from the Haţeg Basin) and numerous postcranial elements (from the Transylvanian Basin) belonging to at least two individuals (ŐSI et al. 2014a). The affinity of the postcranial remains with *Struthiosaurus* was based on the morphology of the proximal half of a humerus being strongly similar to those described from various European localities (ŐSI & PRONDVAI 2013). A dorsal centrum and a fragmentary scapulocoracoid are the only overlapping elements with those of the type of *S. transylvanicus*, but the lack of diagnostic characters on these elements prevent their assignment to this species. The tooth was described as Nodosauridae indet. and shows significant differences compared to those of other ankylosaurs (including *S. austriacus*, *S. languedocensis* and *Hungarosaurus*) in having only six, more or less equally sized, apically pointed cusps separated by deep grooves and surrounded by a marked cingulum. The cusps frequently bear further secondary cusps or small cusples mesiodistally. This tooth is most similar to one isolated tooth published by CODREA et al. (2002) These two teeth suggest, that in the aspect of tooth morphology, at least some of the Haţeg nodosaurids were different from other European members of the clade not only at species but perhaps also at generic level. Besides these assemblages of *Struthiosaurus*, a complete, well-preserved humerus referred to cf. *Struthiosaurus* sp. has been described from the Santonian of Iharkút, western Hungary providing the first evidence for two sympatric ankylosaurs (*Hungarosaurus*, *Struthiosaurus*) in a European continental fauna (ŐSI & PRONDVAI 2013). In addition various other bones from Iharkút, including a partial hip region, might be referable to *Struthiosaurus*. Work on this material is in progress that hopefully will help in clarifying the specific diversity of *Struthiosaurus* in Central Europe.

Struthiosaurus languedocensis
The most recently described species of *Struthiosaurus* is *S. languedocensis* from the lower Campanian of southern France (GARCIA & PEREDA-SUBERBIOLA 2003). It is based on an articulated hip region including the sacrum and most of the pelvic elements, three teeth, four posterior dorsal and one caudal vertebrae and three osteoderms. The main problem in distinguishing this species from the other *Struthiosaurus* species is that the overlapping parts are only the dorsal vertebrae and ribs, the ilium and ischium. In their differential diagnosis GARCIA & PEREDA-SUBERBIOLA (2003) concluded that *S. languedocensis* differs from *S. austriacus* by its robust, parallel-sized ischium that ends distally in a blunt knob. However, the ischium described from the Austrian material was only tentatively identified as this element, and its proximal and distal ends are missing (PEREDA-SUBERBIOLA & GALTON 2001). So, at present, I see that the *S. languedocensis* cannot be unambiguously distinguished from *S. austriacus* or from *S. transylvanicus*. Hopefully, new material helps to clarify this problem.

Besides the discovery of the third *Struthiosaurus* species, various other ankylosaurian material from Campano-Maastrichtian sediments in northern Spain (ASTIBIA et al., 1990; PEREDA-SUBERBIOLA 1993a, 1999, PEREDA-SUBERBIOLA et al. 1995, GARCIA & PEREDA-SUBERBIOLA 2003) and southern France (BUFFETAUT & LE LOEUFF 1991, LE LOEUFF 1991, PEREDA-SUBERBIOLA 1993c) supported the presence of *Struthiosaurus* in western Europe (see Table 1).

Ankylosaur tracks
Isolated Upper Cretaceous ankylosaur tracks have been reported from the Turonian-Coniacian of Altamura, Italy (DAL SASSO 2003, PETTI 2006) suggesting the presence of ankylosaurs in the pre-Santonian Late Cretaceous European archipelago.

The European clade Struthiosaurinae
NOPCSA (1923a) discussed the affinities of *Acanthopholis*, and in an other paper (NOPCSA 1923b:126) he proposed the subfamilies Struthiosaurinae and Ankylosaurinae under the family of Acanthopolidae without any comment. COOMBS (1978) rejected the previously proposed subfamilies and accepted two clades within Ankylosauria: Ankylosauridae and Nodosauridae. KIRKLAND et al. (2013) recognized many similarities among some of the Cretaceous European ankylosaurs and united *Europelta*, *Anoplosaurus*, *Hungarosaurus* and all species assigned to *Struthiosaurus* into the clade Struthiosaurinae. They defined the clade by the following characters to which my comments are as follows:
1) *Narrow predentary*. Although the predentary is unknown in all of these forms, the symphyseal end of the dentary is preserved in all of these genera with a quite short, edentulous part accepting the concave articular surface of the predentary. In *Anoplosaurus* the very end of the dentary is missing, but the position of the first alveolus suggests a short (if any) edentulous part. On the other hand, a relatively short edentulous part (the length of 4-5 alveoli as in *Hungarosaurus* and *Europelta*) anterior to the first alveolus can be observed in other basal ankylosaurs (e.g. *Sauropelta*, *Gargoyleosaurus*, *Sarcolestes*) as well.
2) *A nearly horizontal, unfused quadrate that is oriented less than 30° from the skull roof*. This is not clear. The quadrate of *Europelta* is not nearly horizontal but according to the skull reconstruction of KIRKLAND et al. (2013) it is obliquely positioned (ca. 30-40º relative to the vertical plane) as in many ankylosaurs (e.g. *Pawpasaurus*, *Edmontonia*). The quadrate-paraoccipital-squamosal contact can be observed only in *Europelta* (unfused) and in *Struthiosaurus transylvanicus* (the right one preserved, appears to be fused to me, Fig. 3G).
3) *Mandibular condyles that are 3 times transversely wider than long*. While this is true in *Europelta*, in *Struthiosaurus austriacus* and *S. transylvanicus* the distal quadrate condyles are only two times wider mediolaterally than long anteroposteriorly, in *Hungarosaurus* this ratio is 1.3 (ŐSI 2005, fig:5C, D). Similar ratio (ca. 1.5-2.0) can be observed in various other nodosaurid ankylosaurs (e.g. *Pawpawsaurus*, *Edmontonia*, *Panoplosaurus*).
4) *Premaxillary teeth and dentary teeth that are near the predentary symphysis*. Direct evidence for premaxillary teeth are known only in *Hungarosaurus*. Caution is needed when concluding premaxillary teeth simply on the basis of the presence of dentary teeth close to the symphysis, since, for example, in the right dentary of *Edmontonia* (TMP 98.98.01 housed in the Royal Tyrell Museum, Alberta, Canada) there are no upper teeth opposite to the anteriormost dentary teeth (even if they are worn).
5) *Dorsally arched sacrum*. The synsacrum is known only in *Europelta*, *S. languedocensis* (plus one specimen referred to *Struthiosaurus* sp. by GARCIA & PEREDA-SUBERBIOLA 2003) and in *Hungarosaurus*. In *Anoplosaurus* the sacrum is composed of unfused vertebrae suggesting its subadult ontogenetic status. A slightly dorsally arched synsacrum indeed

present in *Struthiosaurus* and *Hungarosaurus* (as probably in most ankylosaurs) but this is similar to that of the type of *Polacanthus foxii* (PEREDA-SUBERBIOLA 1994). The strongly arched posterior segment of the sacrum of *Europelta* appears to be rather an autapomorphy of this genus.
6) *An acromion process dorsal to midpoint of the scapula-coracoid suture*. This feature cannot be seen in *Europelta* and *S. languedocensis*. In *Anoplosaurus* the acromion process is rather posterodorsal to midpoint of the scapula-coracoid suture. Similar dorsal or slightly posterodorsal position of this process can be seen in *Panoplosaurus* (RUSSELL 1940) as well.
7) *Straight ischium, with a straight dorsal margin*. The ischium is unknown in *Anoplosaurus* and *S. transylvanicus*. It seems to me that the dorsal side of the ischium of *Europelta* (KIRKLAND et al. 2013, fig. 23D, H) is not straight but convex and the distal end of the bone is curved ventrally and seems to be not complete, so this character appears to be ambiguous.
8) *Relatively long slender limbs*. Limb elements of the species referred to Struthiosaurinae are poorly known. The only form with complete fore- and hindlimbs is *Hungarosaurus* where the elongate and gracile limb bones are clearly present. Among the *Struthiosaurus* species, only *S. austriacus* has comparable limb elements. Whereas the femur is relatively slender, compared to *Polacanthus* or *Sauropelta* (PEREDA-SUBERBIOLA & BARRETT 1999), the humerus is quite short and massive (ŐSI & PRONDVAI 2013) as seen also in *Europelta* (KIRKLAND et al. 2013:fig. 21E-H) suggesting that at least the forelimb of *S. austriacus* was not really long and slender but rather short, though the lower arm bones are not preserved.
9) *A sacral shield of armor*. Except for *Europelta* and probably *Struthiosaurus* sp. from Laño, Spain (PEREDA-SUBERBIOLA 1999), there is no evidence for this type of armor among the type material of struthiosaurine forms. Actually this armour type is not the typical sacral shield as seen in some basal nodosaurids (polacanthids of FORD 2000), but a complex of coossified polygons (category 3 of ARBOUR et al. 2011) with large, subequal-sized osteoderms that are tightly sutured together. Similar blocks of coossified, subequal-sized osteoderms are known in an unpublished specimen of a nodosaurid ankylosaur from the Santonian of Iharkút, but still it is not clear if it belongs to *Hungarosaurus* or *Struthiosaurus*. This kind of sacral armour is present in many other forms including *Aletopelta* (FORD & KIRKLAND 2001), *Stegopelta* (BURNS 2008), or *Glyptodontopelta* (FORD 2000).
10) *Erect pelvic osteoderms with flat bases*. Since there is no articulated pelvic armor in any of the taxa referred to this clade, it is quite questionable to use this feature as a diagnostic character. A flat-based, massive, and bomerang-shaped osteoderm with the bases of two conical spikes have been found associated with one of the referred skeletons of *Hungarosaurus*. ŐSI & MAKÁDI (2009) suggested this element to be dorsal to the posterior part of the sacrum but its exact position is still unknown.
Assuming the review of the struthiosaurine characters listed by KIRKLAND et al. (2013), in my opinion, it is problemetic to unite these European species based on these osteological features. At present I cannot accept any of these characters with high confidence to define this clade. Using these characters as a combination of traits might be useful, but the problem is that in case of many characters they are either not preserved or ambiguous due to preservational biases.

Conclusions

Review of the European ankylosaur record indicates that remains until the Valanginian are quite sporadical and some of these fossils are hard to be referred to Ankylosauria. *Hylaeosaurus* is the earlieast ankylosaur with enough diagnostic material to conclude phylogenetic relationships. *Europelta carbonensis* from the Spanish late Albian appears to be a key species of nodosaurid ankylosaurs that can be a kind of missing link between the older and more basal 'polacanthine' and the later more derived 'struthiosaurine' forms. It seems

very probable that European ankylosaurs, at least the Late Cretaceous forms, were members of a monophyletic clade (namely the Struthiosaurinae) originating from a common ancestor existed already in the early Cretaceous. This is supported by the close relationship of *Struthiosaurus* and *Hungarosaurus* (ŐSI & MAKÁDI 2009, THOMPSON et al. 2012), the only two genera from the second half of the European Late Cretaceous. However, chronostratigraphically the closest taxon with enough good material is *Europelta* being at least 25 My older than *Hungarosaurus* and *Struthiosaurus*.

Acknowledgements
This work is dedicated to Prof. Dr. BARNABÁS GÉCZY for his 90th birthday, as a full member of the Hungarian Academy of Sciences, former Head of the Department of Palaeontology of the Eötvös University. Among others, his grandiose work and support helped the author in many cases to reveal the secrets of Hungarian dinosaurs.
The author wishes to thank ZSÓFIA HAJDU (MTA-ELTE Lendület Dinosaur Research Group, Budapest) for her generous help in making the basic figures and the reference list. PETER M. GALTON (University of Bridgeport, Bridgeport, USA), XABIER PEREDA-SUBERBIOLA (Universidad del País Vasco, Bilbao, Spain), and MÁRTON SZABÓ (Hungarian Natural History Museum, Budapest) are thanked for sending pictures on different ankylosaur taxa used in this paper.
This research was supported by the MTA–ELTE Lendület Dinosaur Research Group (Grant no. 95102), Hungarian Scientific Research Fund (OTKA T–38045, PD 73021, NF 84193), Hungarian Natural History Museum and the Eötvös Loránd University.

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Figure captions

Figure 1. Chronostratigraphic distribution of the European ankylosaur taxa in western and eastern Europe.

Figure 2. Ankylosaur remains from the Jurassic and Lower Cretaceous of Europe. A, *Sarcolestes leedsi* left mandible (two pieces) from the Callovian of England in medial view. B, *Priodontognathus phillipsii* left maxilla from the Upper Jurassic or Lower Cretaceous of England in lateral, C, medial view (photo courtesy of X. PEREDA-SUBERBIOLA). D, *Dracopelta zbyszewskii* partial rib cage with armour (holotype) from the Kimmeridgian of Portugal (photo courtesy of X. PEREDA-SUBERBIOLA). E, *Hylaeosaurus armatus* partial skeleton (holotype) from the Valanginian of England (https://en.wikipedia.org/wiki/Hylaeosaurus). F, *Polacanthus foxii* (holotype) hip region with sacral shield from the Barremian of England in dorsal view (photo courtesy of X. PEREDA-SUBERBIOLA, after Hulke 1881). G, *Anoplosaurus curtonotus* left fragmentary dentary from the late Albian of England in dorsal, H, medial view (photo courtesy of X. PEREDA-SUBERBIOLA). I, *Europelta carbonensis* fragmentary skull (holotype) from lower Albian of Spain in ventral, J, dorsal, K, left lateral, L, posterior view (modified after Kirkland et al. 2013, PLoS One).

Figure 3. Ankylosaur remains from the Upper Cretaceous of Europe. A, *Struthiosaurus austriacus* (holotype) partial skull from the lower Campanian of Austria in posterodorsal view. B, *Struthiosaurus austriacus* right dentary from the lower Campanian of Austria in dorsomedial view. C, *Struthiosaurus austriacus* right scapula from the lower Campanian of Austria lateral view. D, *Struthiosaurus austriacus* cervical half-ring osteoderm from the lower Campanian of Austria in anterodorsal view. E, *Struthiosaurus austriacus* ?sacral or ?caudosacral spike from the lower Campanian of Austria in medial view. F, *Struthiosaurus transylvanicus* right fragmentary scapulocoracoid from the Maastrichtian of Romania in lateral view. G, *Struthiosaurus transylvanicus* fragmentary skull (holotype) from the Maastrichtian of Romania in posterior, H, right lateral, I, anteroventral view. J, Nodosauridae indet. ?sacral or ?caudosacral spike from the Santonian of Hungary in medial view. K, hip region in ventral view referred to *Hungarosaurus tormai* from the Santonian of Iharkút. L, hip region of *Struthiosaurus* sp. from the upper Campanian of Spain in dorsal view.

Table 1. Ankylosaur remains from Europe listed in chronostratigraphical order.

Name	Material	Age	Locality	Reference(s)
Deltapodus brodericki	tracks	Aalenian-Bajocian	Yorkshire, England	WHYTE and ROMANO 1994, MCCREA et al. 2001, LOCKLEY et al. 1994
Sarcolestes leedsi	fragmentary left mandible	Middle Callovian	Fletton, England	LYDEKKER 1893, GALTON 1980a, 1983a, b, 1994
Cryptodraco eumerus	right femur	Middle-Upper Oxfordian	Great Gransden, England	(SEELEY 1869, LYDEKKER 1889, GALTON 1980a, 1983a
Dracopelta zbyszewskii	partial rib cage with armour, an articulated partial autopodium	Kimmeridgian	Ribomar, Portugal	GALTON 1980b, 1983a, PEREDA-SUBERBIOLA et al. 2005
Ankylosauria indet.	osteoderms	Kimmeridgian	Rodbourne, Wiltshire, England	DELAIR 1973, GALTON 1983a
Ankylosauria indet.	caudal vertebra	Tithonian	Weymouth, Dorset, England	CASEY 1963, GALTON 1983a
Priodontognathus phillipsii	left maxilla	Upper Jurassic or Lower Cretaceous	Yorkshire or Sussex, England	SEELEY 1875, GALTON 1980c, 1983a
?Ankylosauria indet.	tooth	Upper Jurassic or Lower Cretaceous	Lulworth, Dorsetshire, England	GALTON 1980a, 1983a
Ankylosauria indet.	metapodia and a possible spike-like osteoderm	Berriasian	Cornet, Romania	JURCSÁK and KESSLER 1991, POSMOSANU 2003
Ankylosauria indet.	tracks	Berriasian	Dorset, England	ENSOM 1987, LOCKLEY 1991, LOCKLEY and MEYER 2000, MCCREA et al. 2001
Metatetrapous valdensis	trackway	Berriasian	Bückeburg, northwestern Germany	NOPCSA 1923b, HAUBOLD 1971, MCCREA et al. 2001, HORNUNG and REICH 2014
Hylaeosaurus armatus	two partial skeletons with postcranium and some poorly known skull elements, additional isolated elements	Valanginian	England	MANTELL 1833, 1841, 1849, OWEN 1858, PEREDA-SUBERBIOLA 1993b, BARRETT 1996, CARPENTER 2001b
Hylaeosaurus sp.	isolated postcranial elements	Valanginian	Western Germany	SACHS and HORNUNG 2013
Ankylosauria indet.	tracks	Hauterivian-early Barremian	Gargano, Italy	PETTI et al. 2008, SACCHI et al. 2009
Polacanthus foxii	partial skeleton with postcranium (holotype), partial skeleton including some cranial elements, fragmentary ilium with armour (type of *Polacanthus becklesi* Hennig, 1924), isolated elements	Barremian	Isle of Wight, England; Burgos, Spain	OWEN 1865, HULKE 1882, 1888, BLOWS 1982, 1987, PEREDA-SUBERBIOLA 1993b, 1994, PEREDA-SUBERBIOLA et al. 1999, NAISH and MARTILL 2001
Polacanthus rudgwickensis	partial skeleton with postcranium	Barremian	Sussex, England	BLOWS 1996
Polacanthus sp.	Fragmentary postcranium, isolated elements	Barremian to Aptian	Isle of Wight, Sussex, England; Burgos, Soria, Castellón, Spain	LEE 1843, NOPCSA 1929, PEREDA-SUBERBIOLA et al. 1999, 2007, GASULLA et al. 2003, CANUDO et al. 2004, DELAIR 1982

cf. *Polacanthus* sp.	fragmentary basicranium	Barremian	Isle of Wight, England	NORMAN and FAIERS 1996
Ankylosauria indet.	trackway	early Aptian	Puglia, Italy	PETTI et al. 2010
Europelta carbonensis	two partial skeletons with partial skull and postcranium	early Albian	Ariño, Teruel Province, Spain	KIRKLAND et al. 2013
Anoplosaurus curtonotus	partial skeleton with fragmentary dentary and postcranium	late Albian	Cambridge, England	SEELEY 1879, NOPCSA 1923a, PEREDA-SUBERBIOLA and BARRETT 1999
Ankylosauria indet. the *'Acanthopolis* material'	fragmentary basicranium, three teeth, fragmentary postcranial elements	lowermost Cenomanian	Folkestone, Kent, England	HUXLEY 1867, SEELEY 1869, 1879, LYDEKKER 1888, PEREDA-SUBERBIOLA and BARRETT 1999
Hungarosaurus tormai	Nine partial skeletons and hundreds of isolated elements including both cranial and postcranial material	Santonian	Iharkút, western Hungary	ŐSI 2005, ŐSI and MAKADI 2009, ŐSI et al. 2014b, c
cf. *Struthiosaurus* sp.	humerus	Santonian	Iharkút, western Hungary	ŐSI and PRONDVAI 2013
Struthiosaurus austriacus	Fragmentary basicranium and other cranial elements, dentary teeth, postcranial material of more than one individual	Early Campanian	Muthmannsdorf, eastern Austria	BUNZEL 1870, 1871, SEELEY 1881, PEREDA-SUBERBIOLA and GALTON 1992, 1994, 2001
Struthiosaurus languedocensis	Articulated sacral region including synsacrum and hip elements	?Early Campanian	Villeveyrac, southern France	GARCIA and PEREDA-SUBERBIOLA 20031
Nodosauridae indet.	Osteoderms	Campanian	Hérault, southern France	LE LOEUFF 1992, PEREDA-SUBERBIOLA 1993c
Nodosauridae indet.	Osteoderm Cranial and postcranial remains (most of them still unpublished)	Campanian	Chera, Spain	SANZ 1986, COMPANY 2004
cf. *Struthiosaurus* sp.	Cervical neural arch, two osteoderms	Late Campanian	Hérault, southern France	PEREDA-SUBERBIOLA 1993c
Nodosauridae indet. (*Rhodanosaurus* [*Struthiosaurus*] *ludgunensis*)	caudal centra, rib fragments, osteoderms	Campanian-Maastrichtian	Quarante and Montouliers, southern France	DEPERET 1900, NOPCSA 1929; DE LAPPARENT 1947, 1954 PEREDA-SUBERBIOLA 1993c
Nodosauridae indet.	teeth, rib fragment, humerus, osteoderms	Campanian-Maastrichtian	Var, Ariége, southern France	PEREDA SUBERBIOLA 1993c
Nodosauridae indet.	Osteoderms	Early Maastrichtian	Le Mas d'Azil, southern France	LE LOEUFF 1991, PEREDA SUBERBIOLA 1993c
Struthiosaurus transylvanicus	Posterior part of a skull, some vertebrae, ribs, scapula, osteoderms	Maastrichtian	Haţeg Basin, western Romania	NOPCSA 1915, 1929, PEREDA-SUBERBIOLA and GALTON 1994
Nodosauridae indet.	Tooth in jaw fragment	Maastrichtian	Sânpetru, Romania	ŐSI et al. 2014a
cf. *Struthiosaurus* sp.	Fragmentary limb elements, dorsal centrum	Maastrichtian	Vurpăr, Romania	ŐSI et al. 2014a

	and ribs, right scapula, osteoderms			
Struthiosaurus sp.	Sacral region including synsacrum and hip elements	Maastrichtian	Laño, Spain	GARCIA and PEREDA SUBERBIOLA 2003
Struthiosaurus sp.	Dentary, maxilla fragment, teeth, rib fragments, ulna, osteoderms	Maastrichtian	Laño, Spain	ASTIBIA et al. 1990, PEREDA SUBERBIOLA 1999, PEREDA SUBERBIOLA et al. 1993a, 1995
Nodosauridae indet.	osteoderms	Maastrichtian	Aude, southern France	CLOTTES and RAYNAUD 1983, PEREDA SUBERBIOLA 1993c
Nodosauridae indet.	Teeth	?Maastrichtian	Quintanilla del Coco, Spain	POL et al. 1992
Nodosauridae indet.	Teeth	Late Cretaceous	Taveiro, Portugal	ANTUNES and SIGOGNEAU-RUSSELL 1996
Nodosauridae indet.	Tooth	Maastrichtian	Fontllonga 6, Spain	ALVAREZ SIERRA et al. 1994, ESCASO et al. 2010